BREEDING ECOLOGY AND NEST-SITE SELECTION OF YELLOW-BROWED BULBUL *IOLE INDICA* IN WESTERN GHATS, INDIA

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The breeding biology and nest-site selection of Yellow-browed Bulbul *Iole indica*, an endemic to the Western Ghats and Sri Lanka biodiversity hotspot, was studied in the Silent Valley National Park, Kerala, from 2002 to 2005. Breeding occurred in the dry season from mid-November to the end of April with peak egg-laying in January and February. Nests were open cups placed 0.5-6.2 m from the ground in plants 0.6-8.0 m tall. Birds laid clutches of 2-3 eggs and broods hatched synchronously. Overall nesting period lasted for about a month with 3-7 days for nest construction, 11-13 days for incubation and 12-13 days for nestling period. Mayfield nest success was 17.21%. Predation was the main known cause of nest failure, and mortality was higher during the egg stage compared to nestling stage. Yellow-browed Bulbuls used large number of plants (32 species) as nest substrates. Successful nests were characterised by high nest concealment compared to that of the unsuccessful nests. However, information on the abundance and behaviour of predators and experimental manipulations are required for a comprehensive understanding of nest-site selection process.

Key words: breeding biology, *Iole indica*, life history traits, nesting success, Pycnonotidae, tropical rainforest, Yellow-browed Bulbul

INTRODUCTION

Bulbuls (Family Pycnonotidae) are one of the large groups of passerines of the Old World tropics, widespread in southern Asia, Africa, Madagascar, islands of the Western Indian Ocean (Sibley and Monroe 1990; Fishpool and Tobias 2005). They occupy a broad range of habitats from semi-arid deserts to rainforests, with centre of diversity in the Afrotropical and Sundaic regions. Of the 27 genera currently treated within the Family Pycnonotidae, 11 are exclusively Asian, 14 are restricted to Africa and islands of the Western Indian Ocean while the remaining 2 occur in both continents. The Family comprises nearly 140 species and 355 subspecies (Fishpool and Tobias 2005; Woxvold *et al.* 2009) with several complex taxonomic uncertainties (Pasquet *et al.* 2001; Fishpool and Tobias 2005; Moyle and Marks 2006). Only a few widespread and lowland Pycnonotids have been well-studied, in their native and other introduced ranges. Information on the ecology of mid and higher elevation bulbuls are restricted mostly to natural history notes (Fishpool and Tobias 2005). Moreover, information on the life history traits, including developmental rates and nesting success, for majority of the species is not known. Of the 22 species of bulbuls recorded in India (Rasmussen and Anderton 2005), 8 are seen in southern or peninsular India. Most of these species are common in their habitat and are open-cup nesters. Detailed examination of the breeding ecology of these birds is important to understand the evolution of life history strategies of open-cup nesting birds in the tropics.

The Yellow-browed Bulbul *Iole indica* is an endemic to the Western Ghats and Sri Lanka (Grimmett *et al.* 1999). It is one of the most abundant, uniformly distributed species in the tropical rainforests of Western Ghats at an optimum zone of 1,000-1,500 m (Ali and Ripley 1987; Raman 2003), yet relatively little is known of its biology, compared to that of other bulbul species. They are sedentary residents in moist forests with higher levels of frugivory and generalism in the diet compared to other high altitude species (Ali and Ripley 1987; Fishpool and Tobias 2005; Balakrishnan 2007).

The aim of the present study was to provide a detailed description of the breeding ecology of Yellow-browed Bulbul in southern Western Ghats. The specific objectives were to obtain information on the breeding season, nest dimensions, clutch sizes, developmental periods, breeding success, causes of nest failures and nest-site characteristics.

METHODS

Study area

The study was carried out between December 2002 and May 2005 in the core area of Silent Valley National Park (11° 00'-11° 15' N; 76° 15'-76° 35' E; 90 sq. km; 600-2,383 m above msl), and surrounding buffer zones in the Western Ghats, India. Majority of the study area is covered by the 'West coast tropical evergreen forest', with altitudes ranging from 600 to 1,500 m above msl along the Kunthi river and its tributaries, where the breeding habitat of the species is mainly located. The forest canopy is dominated by large evergreen trees, such as *Cullenia exarillata*, *Canarium strictum*, *Calophyllum elatum*, *Eleocarpus serratus*, *Myristica dactyloides*, *Mesua ferrea*, *Jumbosa munronii*, *Syzigium* spp., *Palaquium ellipticum*, *Persea macrantha* and *Poeciloneuron* sp. The sub-canopy and understorey is dominated by species such as *Clerodendrum viscosum*, *Maesa indica*, *Chloranthus brachystachys*, *Ochlandra travancorica* and *Strobilanthes* spp. The study site receives rains from the south-west (May-September) and the north-east (October-December) monsoons. During the study period, annual rainfall ranged from 4,900 to 8,260 mm, with more than half of it occurring during the south-west monsoon. Mean minimum and maximum daily temperatures during the study were 19.83 °C and 25.78 °C respectively.

Nest searching and monitoring

During the study, nests of Yellow-browed Bulbuls were located by following individuals carrying nesting material or food to the nests and by searching vegetation as described by Martin and Geupel (1993). Once located, the nests were checked everyday with the help of field assistants to determine the time of egg laying, clutch size, start and duration of the development period (incubation and nestling), and fate of the nest. Nests accessible from the ground were monitored using binoculars, while higher nests were checked using a pole and mirror. The clutch initiation dates were determined by direct observation of egg laying or by calculating known hatching dates and mean developmental periods. For calculating the development period, only nests where breeding stage transitions could be observed directly were considered. Nest size parameters, such as inner diameter, external diameter, and height and depth to the nearest centimetre were measured in the field; cup thickness, cup volume and material volume were calculated using these measurements (Soler *et al.* 1998; Balakrishnan 2007). Orientation of the nest around the substrate plant was recorded to the nearest degree using a Suunto MCA-D compass.

Nest-site habitat sampling

During the study, habitats were sampled in 108 Yellow-browed Bulbul nest-sites. Nest height, species, height and girth at breast height (GBH) of the nest substrate were recorded immediately after fledging of the young or predation of a nest. The vegetation structure and other physical variables were quantified within an 11.3 m radius circular plot (0.04 ha) around each nest based on standard methods (James and Shugart 1970; Martin *et al.* 1996). Within each of the plots, tree density (number of all trees >10 cm GBH), mean tree height, mean GBH of all trees, visual estimates of foliage cover at canopy (trees >10 m height), sub-canopy (trees =10 m height), shrub, and ground vegetation layers were measured/calculated. Densities of nest plants, saplings and shrubs were measured within a 5 m radius circular plot (0.008 ha) surrounding the nest. Distance from the nest tree to the adjacent tree, shrub, water and trek path/road was also measured. Nest concealment was estimated visually as a percentage of the nest obscured by foliage, 1 m from the nest in the four cardinal directions and 1 m above the nest. These estimates were averaged to obtain a single percentage for a nest.

Data analyses

Breeding season and clutch size was determined from 153 nests. The breeding seasonality was determined by combining the nesting records of each month during three breeding seasons. The relationship between breeding seasonality and climatic variables were tested using non-parametric Spearman's rank correlation. Climatic data were collected from the Walakkad forest station of the Kerala Forests and Wildlife Department. Variation in nest morphometry in different treatments was compared by analysis of variance (one-way ANOVA). Variations in the nest placement attributes between breeding seasons were tested using Kruskal-Wallis test. Uniform distribution of nest orientations were tested using non-parametric Watson one-sample U^2 test for circular distributions. Watson-Williams test was used to evaluate the hypothesis that successful and failed nests have the same mean orientation (Zar 1999).

Hatching, nestling and breeding success were defined as: the probability that eggs laid would hatch, that hatchlings would fledge, and that eggs laid would survive from laying to fledging, respectively. Nests that produced at least one young were considered as successful. Hatching, nestling and breeding success were calculated as an index of the chick fledged versus eggs laid (Jehle *et al.* 2004). Daily nest survival rates (DSR) were estimated using the Mayfield method (Mayfield 1975). The number of exposure days was calculated from the interval between the day the first egg was laid or the day the nest was found if after laying, and the day of fledging. Daily survival rates and nest success were calculated separately for the developmental periods (incubation and nestling), overall nesting period and breeding seasons. Standard errors for survival rates were calculated based on the methods described in Johnson (1979).

Univariate analyses (*t*-tests) were used to compare nest-site characteristics of successful nest-sites with unsuccessful ones. For these analyses, the data was lumped for all nests due to within-breeding season sample size constraints and means ±SE of untransformed data, are presented for ease of interpretation. All tests were two-tailed, and differences were considered significant at $p<0.05$. Mean ±SD values are reported throughout unless otherwise indicated. All statistical analyses were performed by using SPSS 10.0 (SPSS Inc.) and Oriana 2.0 (Kovach Computing Services).

RESULTS

Start and duration of breeding season

Yellow-browed Bulbul is a resident and early season breeder. Nest building started in mid-November (first

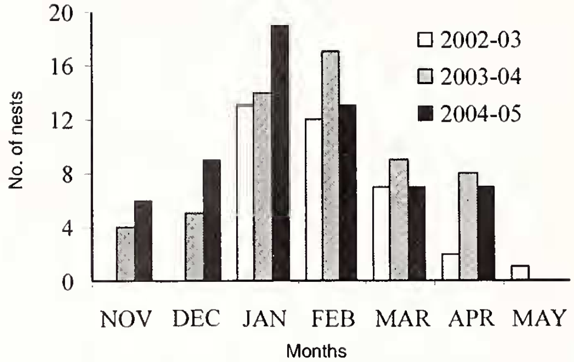

Fig. 1: Breeding season of Yellow-browed Bulbul based on the number of clutches initiated per month during different breeding seasons at Silent Valley National Park

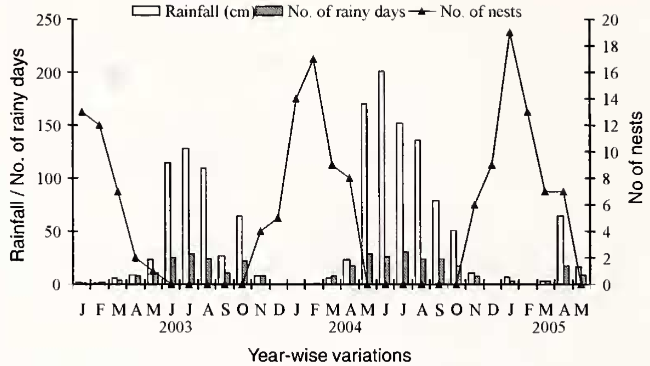

Fig. 2: Relationship between clutch initiations of Yellow-browed Bulbul with monthly rainfall and number of rainy days/month at Silent Valley National Park

observation for the season: November 14, 2003, and November 17, 2004) and laying of the first egg was observed in late November (November 21, 2003 and November 25, 2004). Peak in egg-laying occurred during January and February in all the breeding seasons (Fig. 1). The clutch completion dates for the last nest were observed on May 01, 2003, April 11, 2004 and April 07, 2005. The number of clutches initiated per month was negatively correlated to the monthly rainfall (r_s = -0.826, n=29, *p*=0.001), and number of rainy days per month (r_s = -0.829, n=29, *p*=0.001; Fig. 2).

Nest construction, placement and orientation

Nests of Yellow-browed Bulbuls were open cups (outer diameter: 9.35 ±1.42 cm, inner diameter: 6.41 ±0.87 cm, outer nest height: 7.43 ±0.93 cm, cup depth: 5.07 ±0.62 cm, nest thickness: 2.92 ±0.88 cm, cup volume: 452.54 ±154.41 cu. cm, material volume: 971.89 ±417.51 cu. cm, n=108) made of mostly materials available in the vicinity of the nest sites. The structural constituent of the nests were vine tendrils, dry grass blades, dry leaves of *Cinnamomum sulphuratum*, *Chumnianthus* sp., *Hopea parviflora*, *Lasianthus* spp., *Ochlandra travancorica*, *Oreocnide integrifolia* and inflorescence of *Antidesma menasu*. Innermost lining was made with fibrous roots of pteridophytes and other soft material. 80 out of the 108 nests examined were covered with green moss. There was a significant variation in the morphometry of the nests covered with moss and those lacking a moss decoration (Table 1). Both sexes participated in nest building and construction took 3-7 days to complete (mean = 5.42 ±1.24 days, n=12).

On an average, Yellow-browed Bulbuls placed their nests 1.62 ±1.19 m (range: 0.5-6.2 m, n=108) above the ground at a relative height of 0.64 ±0.13 (range: 0.28-0.93, n=108). The relative height is the height of nest in relation to the tree height on which the nest is placed. There was no significant variation in nest height (Kruskal-Wallis, χ^2=5.780, *p*=0.056), nest plant height (Kruskal-Wallis, χ^2=1.988, *p*=0.370) and relative height (Kruskal-Wallis, χ^2=4.910, *p*=0.086) during the different breeding seasons. Mean nest orientation (μ ± SE) was 168.27 ±22.98° and deviated slightly from random (Length of mean vector, *r* = 0.168; Watson's U^2 = 0.193, *p*<0.05, n=108; Fig. 3).

Clutch size, incubation and nestling periods

Clutch size of Yellow-browed Bulbul ranged from two to three with 92.16% of nests containing two eggs (mean clutch size: 2.08 ±0.27 eggs, n=153). Eggs were laid in the morning, at about 24 hr intervals. Incubation began with clutch completion and hatching was synchronous within broods. Average length of incubation period was 12.06 ±0.64 days (range: 11-13 days, n=18). Nestling period ranged from 12 to 13 days (mean: 12.76 ±0.44 days, n=17). Overall nesting period from the start of incubation was 24.85 ±0.69 days (range: 24-26, n=13).

Table 1: Variation in the morphometry of nests with moss cover and nests devoid of moss of Yellow-browed Bulbul in Silent Valley National Park

Nest size variables	Nest with moss cover (±SD)	Nest devoid of moss cover (±SD)	*F*	p
Outer diameter (cm)	9.95 ±1.05	7.64 ±1.05	111.228	0.001
Inner diameter (cm)	6.65 ±0.79	5.80 ±0.78	24.236	0.001
Outer depth (cm)	6.49 ±0.74	7.77 ±0.75	60.328	0.001
Inner depth (cm)	5.29 ±0.46	4.44 ±0.59	59.139	0.001
Cup thickness (cm)	3.30 ±0.66	1.84 ±0.42	118.861	0.001
Cup volume (cu. cm)	499.54 ±143.21	318.25 ±96.06	38.651	0.001
Material volume (cu. cm)	1140.11 ±342.30	491.27 ±156.84	93.3	0.001

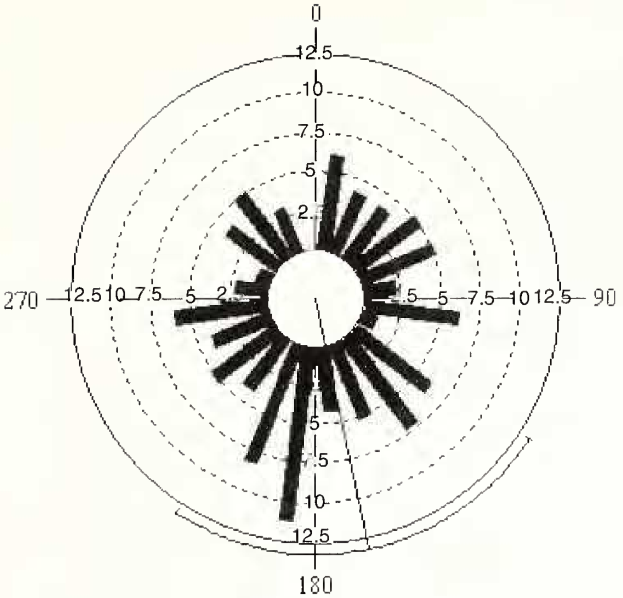

Fig. 3: Nest orientation of Yellow-browed Bulbul in trees used for nesting (n=108 nests, bin width=15°). Dotted circles indicate scale (% of nests)

Nesting success

25 of 108 nests (23.15%) fledged young birds, with successful nests producing 2.12 ±0.33 young. Overall hatching (% eggs hatched), fledging (% hatched chicks fledging) and breeding success (% eggs fledged) were 42.92% (97 of 226 eggs), 54.64% (53 fledged out of 97 hatched) and 23.45%, respectively. Daily survival rates (mean ± SE) were 0.923 ±0.009, 0.949 ±0.011 and 0.932 ±0.007 during the incubation, nestling, and overall nesting periods respectively (Table 2). The Mayfield nest success rate for the entire breeding period was 17.21%. The daily survival rates did not vary between the breeding seasons (Table 3).

Predation was the major cause of nest failure, which is characterised by the complete loss of eggs or nestlings. Of the 83 nest failures, at least 71 nests (>85%) failed due to predation. Predation of eggs and chicks by Common Vine Snake *Ahaetulla nasuta*, White-bellied Treepie *Dendrocitta leucogastra*, and Greater Coucal *Centropus sinensis* were recorded during the study period. Five nests were destroyed by trampling by large vertebrates (Asian Elephant *Elephas maximus*, Sambar *Cervus unicolor*). No brood parasitism was recorded in the clutches examined.

Table 2: Daily nest survival rate and associated variance and nest success of Yellow-browed Bulbul during different reproductive phases, Silent Valley National Park, southern India

Reproductive phase	Exposure days	No. of nests	No. of nest failed	Daily nest survival ± SE	Nest success
Incubation	791	108	61	0.923 ± 0.009	38.17
Nestling	430	47	22	0.949 ± 0.011	50.52
Overall nesting	1221	108	83	0.932 ± 0.007	17.21

Nest-site selection

Yellow-browed Bulbul nests (n=108) were built in at least 32 plant species with more than 52% nests in 6 species (Table 4). The nests without moss decoration were placed in sub-canopy plants such as *Antidesma menasu*, *Callicarpa tomentosa*, *Olea dioica*, *Oreocnide integrifolia* and saplings of *Syzigium* sp., while majority of the nests with moss cover were found in the shrub layer. Nest placement attributes and nest patch characteristics significantly varied between nests covered with moss and those lacking a moss decoration, except for the sub-canopy cover, relative nest height and distance to the trek path/road from the nest (Table 5). However, there was no variation in the success rates between nests covered with moss (23.75%) and those lacking a moss decoration (21.43%). The only significant difference detected between successful and unsuccessful nest-sites was high nest concealment for successful nests (Table 6). Nest orientation also did not vary between the successful (mean vector, μ ±SE = 186.11 ±54.31°, n=25) and failed nests (mean vector, μ ±SE = 163.83 ±24.90°, n=83; Watson-Williams test: $F_{1,106}$ = 0.548, p=0.461).

DISCUSSION

Tropical birds show great heterogeneity of breeding seasons compared to seasonal breeding in temperate species (Moreau 1950; Skutch 1950; Ali and Ripley 1987; Wikelski *et al.* 2000). Food supply, competition, nesting conditions, predation pressure and climatic factors are the ultimate factors known to influence the breeding time. Majority of the pycnonotids occur in the equatorial rainforests and tropical islands, and breed throughout the year and raise several broods (Ali and Ripley 1987; Fishpool and Tobias 2005). Ali and Ripley (1987) reported February to May as the breeding season of Yellow-browed Bulbul. The present study indicates that they start breeding by mid-November and continue throughout the dry season in the Silent Valley National Park. They avoided breeding during the south-west monsoon

Table 3: Daily nest survival rate and associated variance and nest success of Yellow-browed Bulbul during different breeding seasons, Silent Valley National Park, southern India

Breeding season	Exposure days	No. of nests	No. of nest failed	Daily nest survival ± SE	Nest success
2002-2003	265	25	20	0.926 ± 0.016	14.06
2003-2004	476	39	30	0.937 ± 0.011	19.64
2004-2005	480	44	33	0.931 ± 0.012	16.85

months as in the case of other pycnonotids occurring in the area (Balakrishnan 2007; in press). Furthermore, the breeding activities coincide with the general fruiting phenology of the study area, which shows a bimodal fruiting pattern (Balakrishnan 2007). Peak egg laying occurs about one month prior to the peak fruiting during late summer and early south-west monsoon (March-May). Higher levels of frugivory and generalism in the diet could be the reason for the early start of breeding compared to the other high altitude species, such as Square-tailed Black Bulbul *Hypsipetes ganeesa*.

Ali and Ripley (1987) reported that the nests of Yellow-browed Bulbuls are quite unlike that of other pycnonotids and more like a large White-eye's nest. This is true for the nests devoid of moss cover, but nests with moss decoration are larger in size (Table 1) and comparable with that of other bulbul species. More than 92% of nests had two eggs, and the remaining three. Ali and Ripley (1987) also reported the clutch size as two or three (two in Sri Lanka), which is the typical range of most African and Asian species of bulbuls (Fishpool and Tobias 2005). The incubation (12 days) and nestling periods (13 days) fall within the typical range of most species of bulbuls (11-14 days) (Liversidge 1970; Vijayan 1975, 1980; Walting 1983; Ali and Ripley 1987; Hsu and Lin 1997; Krüger 2004; Fishpool and Tobias 2005; Balakrishnan 2007; in press). Overall nesting period from the start of nest construction was about a month. This along with the long breeding season indicates that species raise multiple broods. However, the number of nesting attempts per season was not determined in the present study due to the lack of colour marking of birds.

About 23% nests produced fledglings, which is similar to that of the higher altitude pycnonotids breeding at Silent Valley (Balakrishnan 2007; in press), but higher than that reported for the lowland species, such as White-browed *Pycnonotus luteolus* (13.2%) and Red-vented Bulbuls *Pycnonotus cafer* (8.3%) in southern India (Vijayan 1975, 1980). The Mayfield nest success rate (17.21%) is also higher in Yellow-browed Bulbul than in Grey-headed (10.79%) and Square-tailed Black (12.84%) Bulbuls breeding in the same habitats (Balakrishnan 2007; in press). However, the nest

Table 4: Plant species used as nest substrates by Yellow-browed Bulbul during 2002-2005 at Silent Valley National Park with their frequency, height characteristics and success rate

Plant species	No. of nests (%)	Nest height in m ± SD	Tree height in m ± SD	Relative height	% successful
Lasianthus ciliatus	17	0.82 ± 0.18	1.34 ± 0.26	0.62 ± 0.12	23.53
Lasianthus jackianus	11	0.95 ± 0.24	1.61 ± 0.31	0.60 ± 0.14	27.27
Agrostistachys borneensis	9	0.92 ± 0.16	1.61 ± 0.31	0.58 ± 0.09	22.22
Antidesma menasu	7	3.37 ± 0.79	5.27 ± 1.51	0.65 ± 0.11	28.57
Olea dioica	7	2.72 ± 0.59	4.12 ± 1.58	0.71 ± 0.18	28.57
Cullenia exarillata	6	1.53 ± 0.59	2.18 ± 0.71	0.70 ± 0.08	33.33
Thottea siliquosa	5	1.20 ± 0.52	2.02 ± 1.13	0.60 ± 0.07	20.00
Clerodendrum viscosum	4	4.88 ± 1.10	7.00 ± 1.09	0.69 ± 0.06	25.00
Psychotria nigra	4	1.69 ± 0.23	2.26 ± 0.26	0.76 ± 0.10	25.00
Syzigium sp. sapling	4	1.38 ± 0.89	2.15 ± 1.57	0.66 ± 0.12	0.00
Chloranthus brachystachys	3	0.83 ± 0.06	1.20 ± 0.20	0.70 ± 0.09	33.33
Pavetta indica	3	1.03 ± 0.25	1.90 ± 0.17	0.55 ± 0.13	33.33
Ancistrocladus heyneanus	2	1.10 ± 0.14	1.60 ± 0.14	0.69 ± 0.03	0.00
Cinnamomum sulphuratum	2	1.95 ± 0.64	4.25 ± 1.06	0.50 ± 0.27	0.00
Eurya nitida	2	0.85 ± 0.21	2.25 ± 0.07	0.50 ± 0.01	50.00
Glochidion ellipticum	2	4.55 ± 0.07	6.25 ± 1.06	0.74 ± 0.11	0.00
Knema attenuata	2	0.60 ± 0.14	0.70 ± 0.14	0.86 ± 0.03	0.00
Litsea floribunda	2	1.10 ± 0.42	1.85 ± 0.50	0.59 ± 0.07	100.00
Oreocnide integrifolia	2	3.85 ± 0.21	6.00 ± 0.71	0.65 ± 0.04	0.00
Saprosma glomerata	2	0.65 ± 0.07	0.75 ± 0.07	0.87 ± 0.01	0.00
Actinodaphne lawsonii	1	1.40	2.00	0.70	0.00
Allophyllus cobbe	1	0.90	1.60	0.56	0.00
Callicarpa tomentosa	1	2.80	4.50	0.62	0.00
Daphniphyllum neilgherrense	1	2.70	3.60	0.75	100.00
Elaeocarpus munronii	1	1.60	1.80	0.89	0.00
Hopea parviflora	1	1.50	2.00	0.75	0.00
Myristica malabarica	1	1.10	2.80	0.39	100.00
Neolitsea scrobiculata	1	1.20	2.50	0.48	0.00
Persea macrantha	1	1.20	1.80	0.67	0.00
Sarcococca coriacea	1	0.80	2.20	0.36	0.00
Strobilanthes foliosus	1	1.60	2.00	0.80	0.00
Unidentified shrub	1	1.30	2.50	0.52	0.00

predation rates are slightly higher than that reported for the tropical passerines (71%) (Robinson *et al.* 2000; Stutchbury and Morton 2001). Nest predation was significantly higher during the incubation stage than in the nestling stage. This is opposition to the predictions of parental activity hypothesis (Skutch 1949), which states that nests may suffer higher predation rates during the nestling stage because of increased parental activity and nestling noise. Higher nest predation during incubation has also been reported in several other species (Martin 1992; Mermoz and Reboreda 1998; Balakrishnan 2007). Moreover, variation in nest-site quality can often influence nest predation, and such effects could mask parental activity effects on nest predation (Martin *et al.* 2000). Predation was the major factor limiting breeding success in Yellow-browed Bulbul, as has been reported for other open-cup nesting passerines (Ricklefs 1969; Martin 1993, 1995). Two species of birds (White-bellied Treepie, Greater Coucal) and one snake species (Common Vine Snake) have been confirmed as nest predators by direct observations. Species such as Black-winged Kite *Elanus caeruleus*, Common Rat Snake *Ptyas mucosus* and Jungle Striped Squirrel *Funambulus tristriatus* are also recorded as nest predators of other bulbul species at Silent Valley (Balakrishnan 2007). Other likely predators include several species of small carnivores, corvids, forest raptors, dusky squirrels and colubrid snakes.

Nests with green moss cover were placed in the shrub layer and had a complex vegetation structure surrounding them compared to that of the nests devoid of moss decoration (Table 5). However, variation in nest placement attributes and vegetation structure between nests covered with moss and those lacking moss decoration did not reflect in the nesting success. Thus, a moss decoration in the shrub layer with more foliage cover and lack of moss cover in nests placed higher off the ground with low foliage cover could be different anti-predator strategies in respective microhabitats (Collias and Collias 1984; Hansell 2000). Yellow-browed Bulbuls seem to be generalists in nest substrate selection and they used at least 32 plant species as nest-sites at Silent Valley. Such generalist habits may have disadvantages like increased nest failures because nesting in more forms of vegetation may expose a bird species to a greater variety of predators, thus lessening the likelihood of evolving efficient anti-predator nesting behaviour (Best and Stauffer 1980). However, higher predation rates are reported for high altitude species, such as Grey-headed Bulbul and Square-tailed Black Bulbul, irrespective of the specificity in the substrates selected for nesting (Balakrishnan 2007; in press). Nest concealment was the only habitat variable that acted as a predictor of nest success in Yellow-browed Bulbul. Similar results were obtained when the successful and unsuccessful nests of two groups (nests covered with moss and nests lacking moss cover) were compared separately. However, it is highly unlikely that a single attribute of nesting habitat can determine the fate of the nests given that nest searching techniques, and ability to detect nest-site patches, vary substantially among predators (Chase 2002). Thus, further information on the predator communities and their behaviour, and experimental manipulations are required to understand factors influencing habitat selection and nest success of Yellow-browed Bulbul.

Table 5: Comparison of the nest-site characteristics of nests with moss cover (n=80) and nests devoid of moss cover (n=28, df=106). Shown are means ± SE of untransformed variables and results of *t*-tests

Variables	Nest with moss cover	Nest devoid of moss cover	*t* (p)
Mean tree height (m)	11.80 ± 0.24	9.33 ± 0.35	-5.340 (0.001)*
Mean tree GBH (cm)	52.05 ± 1.69	39.55 ± 1.91	-4.063 (0.001)*
Tree density (#/plot)	59.18 ± 2.19	41.79 ± 2.53	-4.347 (0.001)*
Per cent canopy cover	59.38 ± 1.27	39.46 ± 3.04	-7.142 (0.001)*
Per cent sub-canopy cover	47.69 ± 1.83	52.14 ± 2.11	1.335 (0.185)
Per cent shrub cover	79.31 ± 1.40	57.86 ± 2.79	-7.455 (0.001)*
Per cent ground cover	71.06 ± 1.16	52.50 ± 3.17	-6.868 (0.001)*
Nest height (m)	1.04 ± 0.04	3.29 ± 0.22	15.480 (0.001)*
Nest plant height (m)	1.72 ± 0.08	4.93 ± 0.34	13.634 (0.001)*
Relative nest height	0.63 ± 0.02	0.68 ± 0.02	1.647 (0.102)
Nest plant GBH (cm)	7.46 ± 0.49	33.54 ± 2.97	13.495 (0.001)*
Nest plant density (#/plot)	9.48 ± 2.43	6.68 ± 1.09	-0.669 (0.505)
Sapling density (#/plot)	34.74 ± 1.82	23.18 ± 1.54	-3.590 (0.001)*
Shrub density (#/plot)	153.82 ± 6.04	41.43 ± 5.31	-10.495 (0.001)*
Nest concealment (%)	76.21 ± 1.16	63.64 ± 2.17	-5.365 (0.001)*
Distance to water (m)	47.61 ± 5.51	306.79 ± 47.16	8.879 (0.001)*
Distance to trek path (m)	34.48 ± 9.83	8.10 ± 2.37	-1.577 (0.118)
Distance to adjacent tree (m)	1.39 ± 0.07	2.09 ± 0.16	4.590 (0.001)*
Distance to adjacent shrub (m)	0.70 ± 0.04	1.59 ± 0.14	7.925 (0.001)*

* significant values

Table 6: Comparison of the nest-site characteristics of successful nests (n=25) and unsuccessful nests (n=83, df= 106)

Variables	Successful	Unsuccessful	*t* (p)
Mean tree height (m)	11.23 ± 0.47	11.14 ± 0.26	0.164 (0.870)
Mean tree GBH (cm)	51.33 ± 3.17	48.05 ± 1.62	0.959 (0.340)
Tree density (#/plot)	53.32 ± 3.32	55.07 ± 2.26	-0.389 (0.698)
Per cent canopy cover	56.60 ± 3.17	53.49 ± 1.67	0.884 (0.379)
Per cent sub-canopy cover	45.60 ± 3.78	49.82 ± 1.53	-1.216 (0.227)
Per cent shrub cover	76.20 ± 2.37	73.01 ± 1.89	0.867 (0.388)
Per cent ground cover	67.80 ± 2.66	65.78 ± 1.67	0.598 (0.551)
Nest height (m)	1.65 ± 0.23	1.61 ± 0.13	0.147 (0.883)
Nest plant height (m)	2.62 ± 0.38	2.53 ± 0.19	0.239 (0.812)
Relative nest height	0.64 ± 0.02	0.64 ± 0.02	-0.168 (0.867)
Nest plant GBH (cm)	14.92 ± 2.95	14.01 ± 1.58	0.274 (0.784)
Nest plant density (#/plot)	6.80 ± 1.27	9.34 ± 2.35	-0.584 (0.560)
Sapling density (#/plot)	29.04 ± 2.82	32.55 ± 1.74	-0.996 (0.321)
Shrub density (#/plot)	126.40 ± 12.09	124.17 ± 7.91	0.140 (0.889)
Nest concealment (%)	89.40 ± 1.05	68.00 ± 0.93	11.938 (0.001)*
Distance to water (m)	137.20 ± 39.03	108.06 ± 18.53	0.730 (0.467)
Distance to trek path (m)	19.69 ± 6.03	30.04 ± 9.44	-0.589 (0.557)
Distance to adjacent tree (m)	1.61 ± 0.16	1.56 ± 0.08	0.266 (0.791)
Distance to adjacent shrub (m)	0.88 ± 0.15	0.95 ± 0.07	-0.454 (0.650)

*significant values
Shown are means ± SE of untransformed variables and results of *t*-tests.

CONCLUSION

The Yellow-browed Bulbuls followed the general pattern of life history traits of other high altitude species, but they had a longer breeding season, heterogeneity in nest plant and site selection similar to that of low-altitude bulbuls. The role of habitat attributes, other than nest concealment, is not clear from the study. More information on growth rates, parental care patterns, nest predators and their behaviour, and nest success rates in disturbed habitats would help to understand the geographic diversity of avian reproductive traits and variation in the life history patterns in the tropical-temperate systems.

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